



# Timing of seasonal events is correlated with social network position in a wild mammal

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## Abstract

Across animal systems, abiotic environmental features, including timing of seasonal events and weather patterns, affect fitness. An individual's degree of social integration also has fitness consequences, but we lack an understanding of how abiotic features relate to patterns of individual sociality. A deeper understanding of this relationship could be developed from studying systems where these two links with fitness have already been identified. We explored the relationship between individual social behavior and seasonal timing, seasonal length, and weather patterns. We used social network analysis on a sixteen-year dataset of a wild population of hibernating yellow-bellied marmots (*Marmota flaviventris*). We fit a series of generalized linear mixed models and found that longer growing seasons before winter hibernation and longer winters were associated with increased individual sociality in the following spring. However, later snowmelt was associated with decreased sociality that spring. We found no relationship between individual sociality and various measures of precipitation and temperature. This suggests that seasonal timing and length may be a more important driver of sociality than weather patterns in this system, both as a lag and contemporary effect. Seasonal timing and length may mediate the opportunity or intensity of social interactions. The entwined relationships between the seasonal schedule and weather, and the seemingly contradictory role of winter length and snowmelt, suggests the timing of seasons and its relationship with sociality is complex and further exploration of environment-sociality relationships is required across taxa.

## Significance statement

While the adaptive benefits of social behavior are well studied, less is known about how features of the abiotic environment drive variation in individual social behavior. Given increasing stochasticity in the timing of seasonal events and weather patterns, mapping the environment-sociality relationship will provide important insights to the drivers of sociality in the wild. This is particularly salient for species most vulnerable to climate and environmental change, such as seasonal hibernators, like yellow-bellied marmots (*Marmota flaviventris*). We found that features of seasonal duration were positively associated with increased sociality, whereas the timing of seasonal onset was negatively associated. This work provides empirical evidence towards an important gap in the behavioral ecology literature.

**Keywords** Seasonal timing · Social behavior · Social network position · Environmental variation · Drivers of sociality · Yellow-bellied marmot

## Introduction

The role of abiotic environmental features as a potential driver of animal fitness is well documented. Environmental features like the seasonal timing and length, weather patterns, and resource availability have been linked to a variety of fitness correlates including reproductive success (Pipoly et al. 2013), survival (Requier et al. 2017), and physiological state (Loe et al. 2016) across animal systems. For example, environmental conditions, like high-rainfall during

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the breeding season, affect variability in mean number of eggs produced in superb starlings (*Lamprotornis superbus*; Rubenstein 2011). Wild brook trout (*Salvelinus fontinalis*) experience reduced survival in lower flow and warmer streams (Letcher et al. 2015). Warmer ocean water is associated with decreased mating activity of intertidal barnacles (*Fistulobalanus albicostatus*), resulting in reduced larvae production and smaller populations (Fraser and Cha 2019). Alpine marmots (*Marmota marmota*) have lower rates of juvenile survival during colder winters (Rézouki et al. 2016) and decreased reproductive success with smaller winter snowpacks (Tafari et al. 2013). These studies highlight important associations between the abiotic environment and fitness correlates in wild animals.

The fitness consequences of individual and group social behaviour are also well documented. Social network analysis, when linked with biological attributes, provides specific context to how socially connected individuals and groups are and their associations with fitness (Kurvers et al. 2014; Croft et al. 2016; Philson et al. 2022). Measures of individual sociality, such as degree and strength, quantify direct social connections in the form of the quantity and quality of social partners, whereas measures such as clustering coefficient and embeddedness quantify both an individual's direct and indirect social connections in the form of direct social partners also being social partners themselves and the integration of an individual in their larger network (Ellis et al. 2019). While some species may have positive fitness benefits from increased sociality, either directly or indirectly (Rubenstein 1978; Ellis et al. 2019; Snyder-Mackler et al. 2020), others may experience negative consequences (Gillespie and Chapman 2001; Hughes et al. 2002; Hackländer et al. 2003). For example, more social individuals, measured via clustering coefficient, are associated with increased reproductive success in forked fungus beetles (*Bolitotherus cornutus*; Formica et al. 2012) as social connection fosters opportunity for mating activity. Increased social connectivity was also associated with increased disease transmission in Tasmanian devils (*Sarcophilus harrisi*; Hamede et al. 2009) and longevity in rock hyraxes (*Procapra capensis*; Barocas et al. 2011). Group-level social structure also has fitness implications for the individuals that comprise the group, as residing in certain group social structures can increase or limit social stress and predation pressures (Solomon-Lane et al. 2015; Philson et al. 2022; Costello et al. 2023; Philson and Blumstein 2023a, b). These studies reveal that residing in groups, an individual's position within the group, and group's social structure may have individual fitness consequences.

There is vast literature highlighting the relationship between fitness and features of the abiotic and social environments, yet our understanding of how abiotic environmental factors relate to patterns of individual social position is more nuanced (Pinter-Wollman et al. 2014; Fisher

et al. 2021; Blumstein et al. 2023). Environmental features may influence social interactions, potentially affecting the survival and reproductive success of individuals within the group (Fisher et al. 2021; Blumstein et al. 2023). For example, habitat structure changes the group social structure of sleepy lizards (*Tiliqua rugosa*; Leu et al. 2016) and resource distribution increases individual connectivity and cliquishness in forked fungus beetles (Costello et al. 2022). While these studies highlight the presence of a link between the physical environment and patterns of sociality in some systems, further study is required, especially in wild, free-living systems. This is important because there is increasing variation in timing of seasonal events and weather patterns (Visser and Gienapp 2019). A deeper understanding of this relationship could be developed from studying systems where the link between the physical environment and fitness, and social behaviour and fitness, has already been identified (Fisher et al. 2021).

The yellow-bellied marmot (*Marmota flaviventris*) population at the Rocky Mountain Biological Laboratory (RMBL) in Colorado has been studied annually since 1962. Previous work on this system identified some of the complex environmental drivers of fitness and the mostly negative fitness consequences of social relationships. For example, yellow-bellied marmot survival decreases with decreased snow cover and after summers with low precipitation (Cordes et al. 2020). Later growing season start dates are associated with smaller litters (Downhower and Armitage 1971; Prather et al. 2023). Studies of the relationship between social network measures and fitness correlates show that strong social relationships are often costly for yellow-bellied marmots. More frequent social interactions (i.e., higher values for the strength measure) result in reduced reproductive success of female marmots (Wey and Blumstein 2012) potentially due to the physiological and energetic costs of social relationships. Strong social relationships have also been associated with decreased hibernation survival (Yang et al. 2017) and decreased lifespans across demographic groups (Blumstein et al. 2018). Marmots residing in more connected social groups (i.e., groups that are less likely to fracture in two or more separate groups if social connections are lost) also have decreased reproductive success (Philson and Blumstein 2023a) and summer survival (Philson and Blumstein 2023b). However, in some cases increased sociality, may be beneficial, with more connected adult females having increased summer survival (Montero et al. 2020) and individuals residing in more reciprocal and socially homogeneous groups gaining body mass faster (Philson et al. 2022) and having increased winter survival (Philson and Blumstein 2023b). The context of these environmental and social relationships with fitness, along with the detailed and longitudinal dataset, makes this study system ideal to

contextualize and develop a specific hypothesis to identify potential relationships between environmental factors and the social characteristics of individuals.

We developed an a priori hypothesis for the relationships between physical environment and sociality. We hypothesized that weather patterns and seasonal timing and lengths that enhance individuals' body condition and opportunities for social interaction will increase individual connectedness, the latter of which is typically associated with fitness costs in this system, but is beneficial in specific cases (i.e., summer survival). To quantify the environment-sociality relationship, we used 19 environmental measures of seasonal timing, seasonal length, and weather conditions (categorized into previous growing season length, snowpack depth, winter length, and end of winter, precipitation, temperature) and four attributes of individual sociality, measuring both their direct connections (i.e., degree and strength) and their indirect interactions (i.e., clustering coefficient and embeddedness). These four measures have been previously linked to fitness consequences in this system (Wey and Blumstein 2012; Yang et al. 2017; Blumstein et al. 2018).

With this specific information to ask questions of the environment-sociality relationship, we transformed our broad hypothesis into more specific a priori predictions. We predicted longer growing seasons would be associated with increased individual sociality (e.g., more social partners, more integrated into their broader network) the following spring. The rationale is because longer growing seasons allow for greater fat storage entering hibernation (Armitage et al. 1976; Armitage 1999, 2000), in turn increasing the likelihood of emerging with a better relative body mass (Lenihan and Van Vuren 1996; Howland et al. 2024); individuals can then allocate time to social interactions rather than to foraging and energy conservation (Armitage et al. 1976; Ozgul et al. 2010; Tafani et al. 2013; Cordes et al. 2020). Similarly, we predicted shorter winters would be positively associated with sociality, again facilitating improved relative body mass and time available for social activities. However, not all winters are the same – the depth of the snowpack is an important predictor of hibernacula conditions and hibernation survival in a variety of *Marmota* species (Ozgul et al. 2010; Patil et al. 2013; Tafani et al. 2013; Rézouki et al. 2016; Cordes et al. 2020). We predicted greater maximum winter snowpack depth would be positively associated with sociality because of the increased insulation of deeper snowpacks facilitating less expenditure of stored metabolic energy, again facilitating healthy body mass and time budgets for sociality upon emergence (Patil et al. 2013; Tafani et al. 2013; Rézouki et al. 2016; Cordes et al. 2020). Lastly, we predicted a later end to winter would be negatively associated with sociality due to the decreased time above ground and, consequently, less time for social interactions (Downhower and Armitage 1971; Prather et al. 2023).

For more traditional measures of weather, we predicted cooler and less variable temperatures and increased precipitation in the fall would be associated with increased sociality the following spring as cool temperatures and more precipitation may facilitate plant growth and in turn, permit marmots to store more fat for the winter. This is partly informed by the established association between lower precipitation and decreased survival in this system (Cordes et al. 2020), which may also be attributable to the availability of food resources leading up to hibernation. We predicted warmer, drier springs would be associated with increased sociality as warmer temperatures will melt snow more quickly, and less precipitation will allow marmots to spend more time outside the burrow, both allowing for more time to socialize and greater access to food resources.

In short, we hypothesized that seasonal timings and lengths and weather favorable to body mass gain and social interaction opportunity will be associated with increased individual sociality, which in this system is typically associated with fitness costs, but is beneficial for summer survival.

## Materials and methods

### Study system

The yellow-bellied marmots around RMBL (38°57'N, 106°59'W; ca. 2900 m elevation) are facultatively social and harem-polygynous, living in matrilineal colonies with one or a few territorial males (Frase and Hoffmann 1980; Armitage 1991; Olson and Blumstein 2010). Marmots are active for around five months annually (early mid/late-April to mid-September), hibernating over winter (socially or solitarily) and mating soon after emerging from hibernation. New pups emerge and yearlings disperse around late-June/early-July. Nearly half of all females and most males disperse as yearlings, typically out of the study area (Armitage 1991). Marmots spend the summer months developing body fat reserves in preparation for hibernation and avoiding predation – both of which have relevance for sociality in the form of time budgets (Armitage 1999; Pollard and Blumstein 2008). Resident marmots are observed and repeatedly live trapped during their active season (i.e., when they are not hibernating) with virtually all individuals in our study population uniquely marked, permitting accurate identification of interacting individuals. Body mass was recorded throughout the year at every trapping event. This data was used to calculate best linear unbiased predictions (BLUPs) by fitting linear mixed effects models from the repeated body mass recordings for yearlings and adults from 2002–2021 to predict 1 June and 15 August body mass, as these are dates proxies for early and late season body mass (see Maldonado-Chaparro et al. 2015b; Kroeger et al. 2018; Heissenberger

et al. 2020; Philson et al. 2022 for details on our BLUPs). Social interactions were recorded during hours of peak activity over the entire active season from distances that limited the observer effect and then classified using a detailed ethogram described in Blumstein et al. (2009). The initiator and recipient, time, location, and type of each interaction is recorded. Some 79% of interactions are between identified individuals. We excluded interactions where an individual could not be identified (due to the interacting individuals' posture or visual obstructions) from our data, which should not significantly influence social structure (Silk et al. 2015). We only include individuals observed or trapped more than five times in a year to eliminate individuals dispersing through the study area (Wey and Blumstein 2012; Fuong et al. 2015; Yang et al. 2017; Blumstein et al. 2018). It was not possible to record data blind because our study involved focal animals in the field.

### Social networks

Marmots share space with a subset of all possible individuals within their colony area. We defined social groups based on space-use overlap (two individuals seen or trapped at the same location and time, or observed using the same burrow, within one-day intervals). To define social groups, we used space-use overlap to calculate simple-ratio pairwise association indices (Cairns and Schwager 1987) using SOCPROG (version 2.9; Whitehead 2008) for adults and yearlings for each year (pups were not included due to mid-season emergence and mostly interacting with each other and their mother). We used the random walk algorithm Map Equation (Csardi and Nepusz 2006; Rosvall and Bergstrom 2008; Rosvall et al. 2009) to identify social group membership from these simple-ratio pairwise association indices. While Map Equation assigns each individual to only one social group, this can exclude key social connections, such as those with adult males. Because adult males often mate with females from multiple matrilineal groups and have important interactions with members of multiple groups, we added adult males to each social group for which they had at least one social interaction with a member of that group to enable more accurate social network measures. However, each year, a male's network measures were only calculated from their originally assigned group.

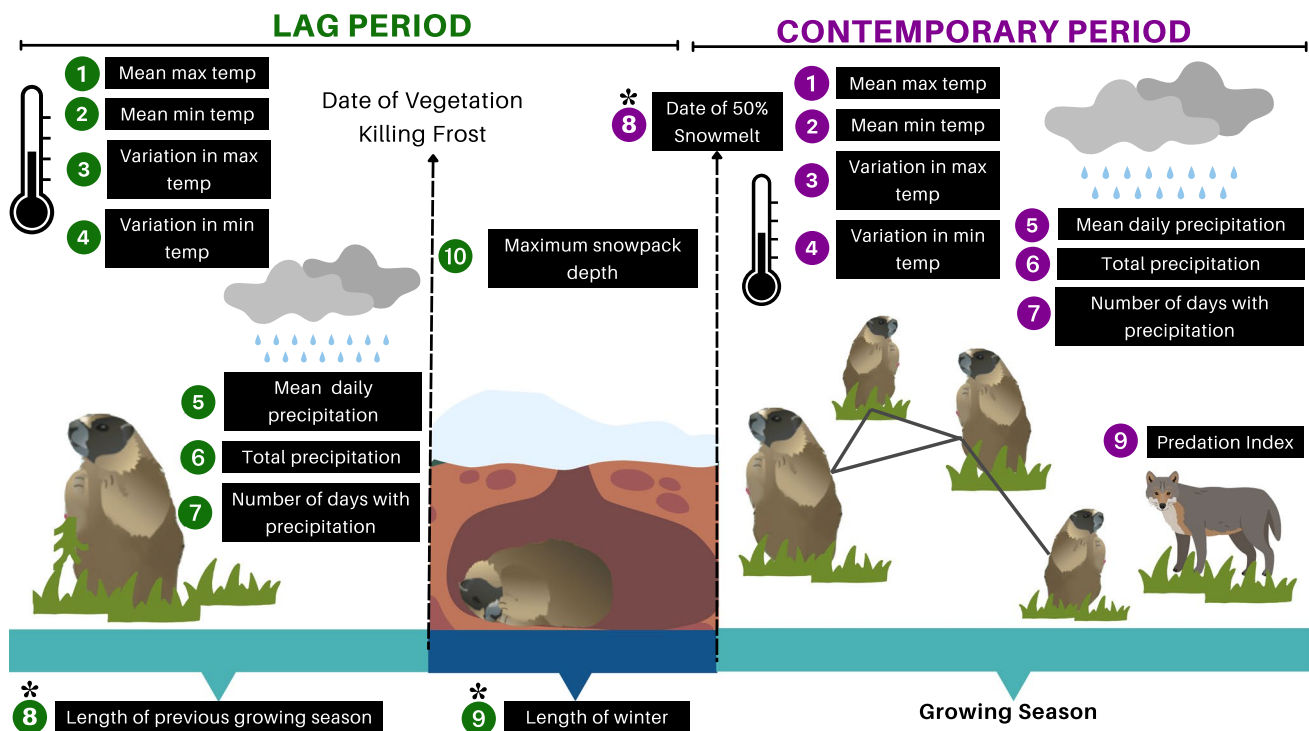
With these group assignments, we constructed directed and weighted social networks based on affiliative interactions (e.g., greeting, allogrooming, play) using the R (version 4.1.2; R Development Core Team 2023) package "igraph" (version 1.2.11; Csardi and Nepusz 2006). We focused on affiliative social interactions because they relate to marmot fitness (Wey and Blumstein 2012; Fuong et al. 2015; Yang et al. 2017; Blumstein et al. 2018; Philson and Blumstein 2023a, b) and because they comprised 88% of all

social interactions. Social networks consisted of yearling and adult females and males and of social interactions occurring from emergence from hibernation (mid-April) through the end of June as a majority of social interactions occur during this timeframe and vegetation growth impairs observations later in the active season. Social networks were constructed from 33,479 social interactions between 666 unique individuals in 210 social groups from 2003–2020. Group sizes ranged from 3 to 31 individuals with a mean of 13.34 individuals ( $SE = 0.302$ ).

We calculated four social network measures to quantify individual social position and connectivity. We selected these measures because of their established relationship to fitness in past studies both within this system (Wey and Blumstein 2012; Yang et al. 2017; Blumstein et al. 2018) and others (Hamede et al. 2009; Barocas et al. 2011; Formica et al. 2012; Ellis et al. 2019). Degree quantifies the number of social partners an individual has (Flack et al. 2006; Blumstein et al. 2009). Strength quantifies the number of social interactions an individual engages in (Wasserman and Faust 1994; Montero et al. 2020). Clustering coefficient quantifies an individual's local cliqueness with their direct social partners (i.e., whether an individual's direct connections are also connected to each other; Wasserman and Faust 1994; Lehmann et al. 2015). Embeddedness quantifies how integrated into their social group an individual is (see Moody and White 2003 for equation; Blumstein et al. 2009). Individuals with higher values for embeddedness have more direct social partners and are a central individual in their local network with their direct partners also being well connected, directly and indirectly themselves. Our estimates of the measures' reliability are facilitated by our behavioral observations of marmots across their entire active season (mean number of observations per individual across years = 28.81, range of each year = 6.79–75.14) and low rate of unknown individuals involved in social interactions (Silk et al. 2015; Davis et al. 2018; Sánchez-Tójar et al. 2018). Because group size inherently influences these social network measures, we included group size as a fixed effect in all models to account for this (see "Data analysis" subheading).

### Environmental measures

We calculated environmental measures by quantifying aspects of weather patterns (i.e., temperature, precipitation), seasonal timing and length, and predation pressures (Fig. 1). Each environmental measure was selected for its relevance and applicability in this system and we developed a priori prediction for each measure. We calculated two suites of these environmental measures, a lag period (from the previous active season/winter) and a contemporary period (from the spring of the year for which social networks were calculated) (Prather et al. 2023). Temperature and precipitation



**Fig. 1** Conceptual figure illustrating the environmental measures used in each period. Asterisks identify statistically significant environmental variables (Table 1; Fig. 2)

data comes from the weather station located at the center of our study sites. Snowmelt and predation data was collected in the field annually for each colony area (Martin et al. 2014; Cordes et al. 2020; Nash et al. 2020).

The lag period had ten environmental measures. For the months of July–September that preceded the spring social networks we calculated, (1) mean maximum temperature ( $^{\circ}\text{C}$ ), (2) mean minimum temperature, (3) variance in maximum temperature, (4) variance in minimum temperature, (5) mean daily precipitation (rain or snow; inches), (6) total precipitation, and (7) number of days with precipitation (Travis and Armitage 1972; Inouye et al. 2000; Cordes et al. 2020). The (8) growing season length of the previous active season was defined as the date of 50% snowmelt at each colony area to the date of the first vegetation killing frost ( $-3^{\circ}\text{C}$ ; Inouye 2000) in the valley (Blumstein 2013; Martin et al. 2014; Cordes et al. 2020). We also calculated the (9) length of winter from the date of the first vegetation killing frost to the date of 50% snowmelt the following year at each colony area and the (10) maximum snowpack depth (Cordes et al. 2020).

The contemporary period had nine environmental measures. For the months of April–June of the year that social networks were calculated for, (1) the mean maximum temperature, (2) mean minimum temperature, (3) variance in maximum temperature, (4) variance in minimum temperature, (5) mean daily precipitation, (6) total precipitation, and (7) number of days with precipitation (Travis and Armitage

1972; Inouye et al. 2000; Cordes et al. 2020). Additionally, we calculated the (8) date of 50% snowmelt to tease apart the length of winter and the ending of winter/start of the growing season as they could have opposing relationships with sociality (Johns and Armitage 1979; Martin et al. 2014; Cordes et al. 2020). Lastly, we fitted (9) predation index as a binary variable calculated by whether the number of predators observations at that colony was below or above the median number of predator observations across all colony areas in that year (Armitage 1982; Nash et al. 2020). We include a predation index in the contemporary period models because of the strong evidence for predation pressures as a driver of individual sociality (Rubenstein 1978; Armitage 1999, 2014), and therefore we want to evaluate the association between predation pressure and individual sociality relative to attributes of the physical environment to assess the potential role of predation in this system.

## Data analysis

To test the relationship between attributes of individual sociality, seasonal timing and length, and weather patterns, we first fitted two suites of linear models that correspond with the lag and contemporary periods described above. All continuous variables, except degree, were standardised (mean-centered and divided by one SD using the “scale” function in base R; (Becker et al. 1988) to facilitate comparisons



between models. Strength, clustering coefficient, embeddedness, and group size were  $\log_{10}$  transformed before scaling. We employed no other transformations. Models were fit using “lme4” (Bates et al. 2014, 2015a, b) and model assumptions were checked after fitting. The models for degree were fit with a Poisson distribution and a bobyqa optimizer with 20,000 iterations. Despite strength also being a count variable, we could not accurately fit strength as a Poisson distribution, and therefore strength, clustering coefficient, and embeddedness were all fitted as linear mixed models. There was no significant multicollinearity between any of our fixed effects ( $VIF \leq 5$ ).

In addition to the environmental measures fitted in the lag and contemporary period models, both suites of models also included individual age, body mass, and the size of their social network (n individuals) as fixed effects. The drivers of individual sociality in this system are multicausal and previous studies have suggested age (Wey and Blumstein 2010; St. Lawrence et al. 2022), body mass (Ozgul et al. 2010; Armitage 2014; Kroeger et al. 2018), and social group size (Wey and Blumstein 2012; Maldonado-Chaparro et al. 2015a) have important links with sociality. Individual social connections are also a potential driver of mass gain rate in this system (Philson et al. 2022). Thus, we include body mass as a fixed effect because it could be a mediator of the environment-sociality relationship. 15-August mass was fit for the lag period models and 1-June mass for the contemporary period models (as estimated with BLUPs; Ozgul et al. 2010; Kroeger et al. 2018) as these dates align with the period we were quantifying.

In both the lag and contemporary period suites of models, Individual ID and year were included as random effects to account for annual demographic differences (Maldonado-Chaparro et al. 2015b; Kroeger et al. 2018; Heissenberger et al. 2020) and individuals observed over multiple years. Models for the lag period had 762 observations consisting of 466 unique individuals in 111 social groups across 14 years. Models for the contemporary period had 842 observations consisting of 510 unique individuals in 123 social groups across 16 years. The lag period has two fewer years of data as we did not have marmot colony specific environmental data in 2001 or 2009 (see Supplementary Table 1 and 2 for these initial model results).

To better understand the relative importance of the environmental variables for individual sociality, we identified the variables that were statistically significant in the lag and contemporary period models, interpreted as  $P < 0.05$ , and placed these variables into one model, per measure of sociality. This final combined suite of models included (1) the growing season length and (2) the length of winter from the models for the lag period, (3) the date of 50% snowmelt from the models for the contemporary period (see Supplementary Fig. 1 and 2 for inter- and intra-year variation in

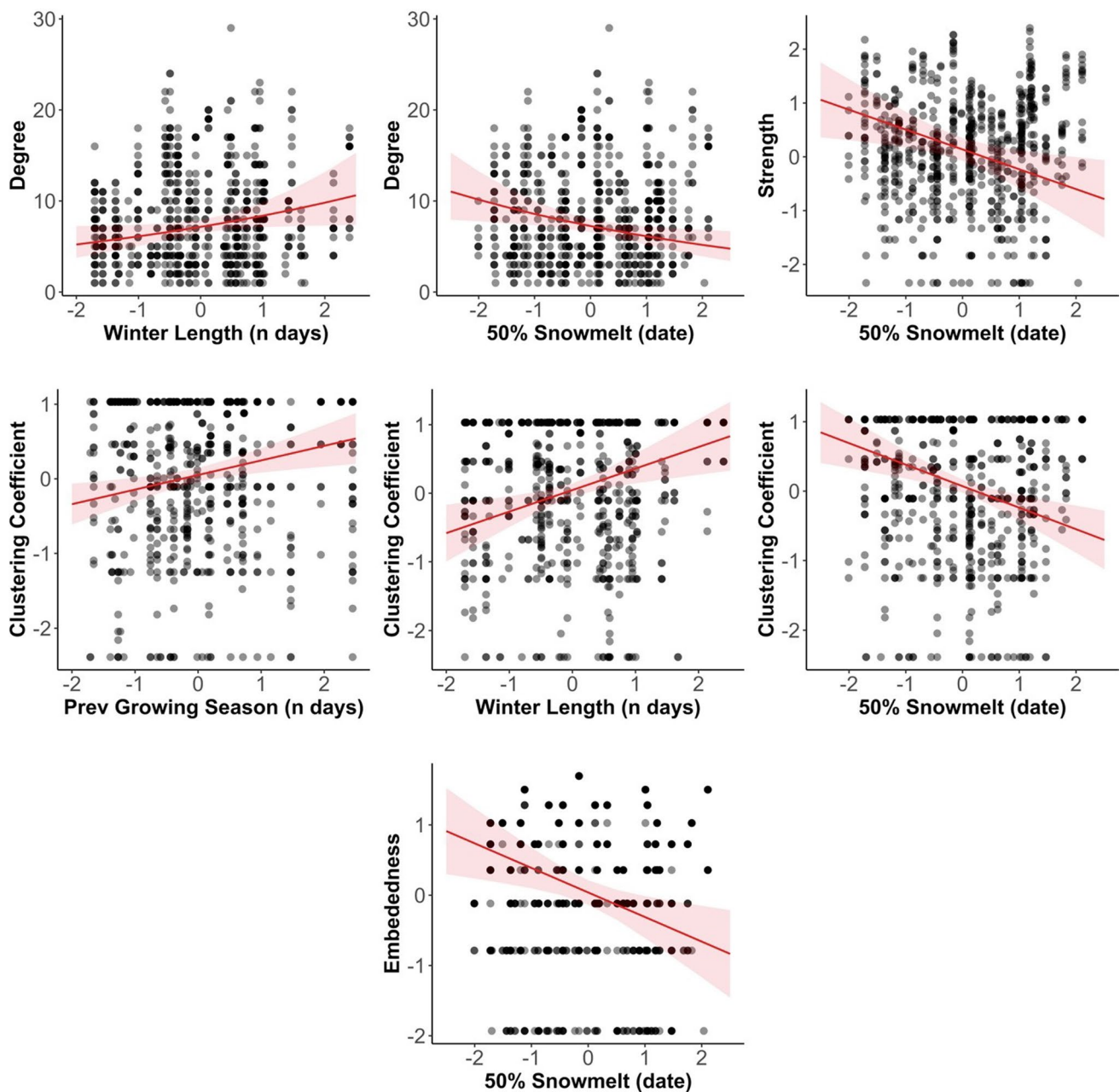
these environmental measures). No other environmental variables were statistically significant in the original two suites of models. Age, body mass, and group size were maintained as fixed effects in these final combined models (as they were statistically significant). Individual ID and year were also maintained as random effects in these final combined models. However, these final combined models experienced some VIF issues (i.e.,  $> 6$ ). For the degree, strength, and embeddedness models, we removed growing season length (because it had the largest VIF value). After removal, all subsequent variables to have a  $VIF < 5$ . These final combined models had 708 observations consisting of 432 unique individuals in 109 social groups across 14 years, except for clustering coefficient, which could not be calculated for some individuals, and thus had 648 observations consisting of 416 unique individuals in 103 social groups across 14 years.

We calculated (using “partR2”; Nakagawa and Schielzeth 2013; Stoffel et al. 2021, 2022) the marginal and conditional  $R^2$  values for each model to estimate variance explained by all the fixed effects and all the fixed and random effects for each model (Table 1). We calculated the semi-partial marginal and conditional  $R^2$  that estimate variance explained by each fixed effect alone (Table 1). We estimated 95% confidence intervals for our  $R^2$  values using 100 parametric bootstrap iterations. We plotted marginal effects for each significant relationship using “ggplot2” (version 3.4.1; Wickham 2016) and “sjPlot” (2.8.12; Lüdtke 2022) (Fig. 2).

## Results

We found that seasonal timing and length, not weather patterns, had a statistically significant relationship with all four of our social network measures (Table 1; Fig. 2). Winter length was positively associated with degree ( $B = 0.158$ ;  $p = 0.036$ ;  $SE = 0.075$ ) and clustering coefficient ( $B = 0.314$ ;  $p = 0.008$ ;  $SE = 0.101$ ). The length of the previous growing season was positively associated with clustering coefficient ( $B = 0.196$ ;  $p = 0.005$ ;  $SE = 0.066$ ). The date of 50% snowmelt was negatively associated with degree ( $B = -0.168$ ;  $p = 0.01$ ;  $SE = 0.065$ ), strength ( $B = -0.369$ ;  $p = 0.018$ ;  $SE = 0.138$ ), clustering coefficient ( $B = -0.31$ ;  $p = 0.002$ ;  $SE = 0.086$ ), and embeddedness ( $B = -0.262$ ;  $p = 0.031$ ;  $SE = 0.111$ ).

June body mass (the contemporary period) had a negative statistically significant relationship with each of the four social network measures whereas August body mass (the lag period) had a positive statistically significant relationship with three of the four social network measures (i.e., degree, strength, and embeddedness; Table 1). Age had a negative statistically significant relationship with strength ( $B = -0.124$ ;  $p = 0.016$ ;  $SE = 0.051$ ) but a



**Fig. 2** Statistically significant relationships (plotted as marginal effects) between the network measures for individual sociality and the attributes of the physical environment (with 95% CIs). Both the response and predictor variables are scaled (mean-centered and

divided by one SD). Fig. was generated with R package “sjPlot” (Lüdtke 2022). Darker points indicate more overlaid data whereas lighter points indicate less overlaid data

positive statistically significant relationship with clustering coefficient ( $B = 0.116$ ;  $p = 0.044$ ;  $SE = 0.057$ ). Group size had a positive statistically significant relationship with degree, strength, and embeddedness, and a negative statistically significant relationship with clustering coefficient (Table 1).

On average, the four models explained 26.1% (range = 12.7%—38.9%) of the marginal variance and 40.1% (range = 20.4%—48.6%) of the conditional variance. Marginal and conditional semi-partial  $R^2$  values for each fixed effect can be found in Table 1.

**Table 1** Model estimate, standard error, P value, marginal and conditional part R<sup>2</sup>, and marginal and conditional semi-partial part R<sup>2</sup> values for the final combined models. Values in bold represent statistical significance (*P* < 0.05). In addition to estimated part R<sup>2</sup> and semi-partial part R<sup>2</sup> values, estimated 95% confidence intervals based on 100 parametric bootstrap iterations are reported in parentheses. Growing season length was removed for VIF issues from three of the four models

	Intercept		Growing Season Length	50% Snowmelt Date	June Mass	August Mass	Age	Group Size
	Est. ± SE	P Value						
Degree	Est. ± SE	1.993 ± 0.05	-	-0.168 ± 0.065	-0.295 ± 0.037	0.174 ± 0.029	-0.005 ± 0.029	0.358 ± 0.023
	P Value	< <b>0.001</b>	-	<b>0.01</b>	< <b>0.001</b>	< <b>0.001</b>	0.864	< <b>0.001</b>
	Marginal R <sup>2</sup>	0.389 (0.351 – 0.404)	0.014 (0 – 0.102)	0.019 (0 – 0.114)	0.04 (0 – 0)	0.028 (0 – 0)	0.001 (0 – 0.129)	0.001 (0 – 0.129)
Strength	Conditional R <sup>2</sup>	0.486 (0.403 – 0.559)	0.111 (0 – 0.224)	0.116 (0 – 0.229)	0.137 (0.014 – 0.248)	0.125 (0.001 – 0.237)	0.097 (0 – 0.211)	0.316 (0.218 – 0.407)
	Est. ± SE	0.146 ± 0.108	0.203 ± 0.166	-0.369 ± 0.138	-0.469 ± 0.07	0.32 ± 0.055	-0.124 ± 0.051	0.116 ± 0.039
	P Value	0.205	0.249	<b>0.018</b>	< <b>0.001</b>	< <b>0.001</b>	<b>0.016</b>	<b>0.003</b>
Clustering Coefficient	Marginal R <sup>2</sup>	0.198 (0.152 – 0.3)	0.025 (0 – 0.15)	0.022 (0 – 0.148)	0.044 (0 – 0.167)	0.029 (0 – 0.154)	0.01 (0 – 0.137)	0.023 (0 – 0.148)
	Conditional R <sup>2</sup>	0.442 (0.368 – 0.555)	0.27 (0.188 – 0.407)	0.267 (0.185 – 0.404)	0.289 (0.208 – 0.423)	0.274 (0.192 – 0.41)	0.255 (0.172 – 0.394)	0.267 (0.185 – 0.405)
	Est. ± SE	0.047 ± 0.049	0.196 ± 0.066	0.314 ± 0.101	-0.31 ± 0.086	-0.233 ± 0.08	-0.026 ± 0.062	0.116 ± 0.057
Embeddedness	P Value	0.361	<b>0.008</b>	<b>0.002</b>	<b>0.004</b>	0.676	<b>0.044</b>	< <b>0.001</b>
	Marginal R <sup>2</sup>	0.127 (0.094 – 0.187)	0.019 (0 – 0.089)	0.023 (0 – 0.093)	0.014 (0 – 0.085)	0 (0 – 0.072)	0.005 (0 – 0.077)	0.049 (0.013 – 0.116)
	Conditional R <sup>2</sup>	0.204 (0.107 – 0.315)	0.096 (0 – 0.212)	0.103 (0.003 – 0.219)	0.091 (0 – 0.207)	0.078 (0 – 0.194)	0.082 (0 – 0.199)	0.126 (0.026 – 0.242)
	Est. ± SE	0.031 ± 0.085	0.22 ± 0.131	-0.262 ± 0.111	-0.396 ± 0.063	0.178 ± 0.049	-0.013 ± 0.046	0.486 ± 0.034
	P Value	0.727	0.121	<b>0.031</b>	< <b>0.001</b>	< <b>0.001</b>	0.778	< <b>0.001</b>
	Marginal R <sup>2</sup>	0.331 (0.286 – 0.407)	0.012 (0 – 0.11)	0.014 (0 – 0.111)	0.034 (0 – 0.13)	0.008 (0 – 0.106)	0 (0 – 0.099)	0.186 (0.131 – 0.27)
Conditional R <sup>2</sup>	0.472 (0.397 – 0.559)	0.154 (0.054 – 0.278)	0.155 (0.056 – 0.28)	0.175 (0.077 – 0.297)	0.149 (0.049 – 0.275)	0.142 (0.041 – 0.268)	0.327 (0.241 – 0.428)	



## Discussion

When exploring the relationship between individual sociality and attributes of the weather patterns and seasonal timing and length, we found modest relationships for three attributes of seasonal timing and length. We showed that a longer growing season before winter hibernation was associated with an increase in an individual's connectedness within their social clique (i.e., clustering coefficient) the following spring, supporting our a priori prediction. Contrary to our a priori prediction, we found that longer winters were also associated with increased sociality (i.e., degree and clustering coefficient) in the following spring. However, we found that later snowmelt date was associated with a decrease in sociality that spring (i.e., degree, strength, clustering coefficient, and embeddedness), supporting our a priori prediction. We found no relationship between environmental measures quantifying weather patterns, such as precipitation and temperature, and individual sociality, rejecting our a priori predictions. This lack of a significant association suggests that seasonal timing and length, more so than weather patterns, may be one of many important drivers of animal sociality and relationships.

The association between a longer growing season before hibernation (lag period) and increased sociality the following spring (contemporary period) could be due to an increase in available metabolic energy (Ozgul et al. 2010; Canale et al. 2016). Fat storage is an important predictor of winter survival in hibernating mammals (Nedergaard and Cannon 1990; Humphries et al. 2003) and yellow-bellied marmots can lose up to 40% of their body mass during hibernation (Armitage 2014). For *Marmota* species, a longer growing season allows for more fat accumulation (Ozgul et al. 2010; Tafani et al. 2013; Rézouki et al. 2016), increasing both the likelihood of hibernation survival and individual body mass when emerging the following spring (Armitage 1994; Armitage et al. 1976; Lenihan and Van Vuren 1996; Ozgul et al. 2010). Thus, marmots with larger spring body mass (as a function of their body mass before hibernation) may have to allocate less time and energy to foraging, allowing more resources to engage in social interactions (Ozgul et al. 2010; Blumstein et al. 2023).

The correlation between longer winters and increased individual sociality has a less simple explanation and seems contradictory to other findings at first glance. Seemingly, longer winters (i.e., marmots hibernating longer) would require marmots to use more metabolic energy to stay warm, depleting fat reserves resulting in emergence with less body mass the following spring (Ozgul et al. 2010; Tafani et al. 2013; Rézouki et al. 2016). Lower metabolic energy in spring could in turn result in less individual sociality. Contrary to our hypothesis that longer winters will

be correlated with decreased sociality (via less body mass/metabolic energy to interact in spring), we found that longer winters were correlated with increased sociality. Our results, however, did show a largely positive relationship between previous fall body mass (of the lag period) and the following spring's sociality, and a largely negative relationship between the spring's body mass (of the contemporary period) and spring sociality. We additionally fitted interaction terms between the environmental variables and June and August body mass in the final combined models, which further support the direction and statistical significance of the relationship with body mass (Supplementary Table 3). Taken together, these two results suggest entering hibernation with a large body mass increases sociality the following spring whereas emerging in spring with poor body mass (potentially due to the length or severity of winter) decreases sociality that spring as less metabolic energy is available for social interactions.

However, this logic for body mass is complicated by two factors, at least in this system. First, winter length is not the only factor contributing to hibernation's metabolic energy demands. Deeper snowpacks serve as an insulating blanket, shielding hibernacula from the harsh winter weather above the snow (Ozgul et al. 2010; Cordes et al. 2020). In Alpine marmots, colder winters and thinner snowpacks has a negative association with winter survival (Rézouki et al. 2016) and reproductive success the following year (Tafani et al. 2013), demonstrating how winter conditions have impacts on spring biology. Thus, we fitted the initial lag models with maximum snowpack depth as a covariate. Snowpack depth did not emerge as a statistically significant predictor in these models, potentially complicating this explanation when additionally considering sociality. Second, our a priori prediction stated that longer winters would be negatively associated with sociality because marmots would have less time to socialize if they emerged later in the spring. A majority of social interactions happen in the first 5–6 weeks after emergence. Yearling dispersal and pup emergence starts in late-June and continues into July. Individuals may overcompensate and become more social if they emerge later to maintain nominal social bond formation and timing of mid-active season life history events. Thus, we had fitted the date of 50% snowmelt as a covariate because this measure generally marks the end of winter in our system (Van Vuren and Armitage 1991; Blumstein 2009). However, the date of snowmelt had a relationship that was opposite these potential explanations.

We found later snowmelt was associated with being less social, suggesting it was not just the length of winter that mattered, but also the timing of winter's end. The explanation may again be tied to body mass, as indicated by the negative relationship between spring body mass and spring

sociality; later snowmelt may mean a longer hibernation which may result in less fat reserves when they emerge in the spring (Ozgul et al. 2010; Tafani et al. 2013; Rézouki et al. 2016). This association is also observed in Alpine marmots (Canale et al. 2016) and other mammals (Kautz et al. 2020; Wells et al. 2022). However, as just discussed, body mass as a potential explanation is nuanced and complicated by other environmental factors, like snowpack depth and snowpack density (Inouye et al. 2000; Ozgul et al. 2010; Cordes et al. 2020; Prather et al. 2023). Our results may reflect how environmental change and shifts in seasonal timing and length are impacting life-history traits in this system. In 2000, yellow-bellied marmots emerged 38 days earlier than in 1977, apparently in response to warmer spring air temperatures (Inouye et al. 2000). Later emergences may be a mismatch to current conditions and lead to fitness and energetic deficits (Visser and Gienapp 2019; Kucheravy et al. 2021), which underlie sociality in this system. Overall, these findings support our overall a priori hypothesis environmental features favorable to body mass and social interaction opportunity are associated with increased individual sociality.

A theme woven through these potential explanations is how environmental change and seasonal shifts influence summer and winter survival (Sæther and Bakke 2000; Gailard and Yoccoz 2003; Prather et al. 2023) because population densities are associated with social group size (Carneiro 1967; Griffiths and Magurran 1997). For example, population size is associated with group size, and group size is strongly associated with individual social network measures (Wasserman and Faust 1994), particularly in our system (Maldonado-Chaparro et al. 2015a). In this system, winter survival is largely driven by conditions during the preceding active season and the impact of continued environmental change, and seasonal shifts are likely to be mainly negative, whereas summer survival is likely to be positively impacted (Cordes et al. 2020). The pathway for how variation in the environment drives variation in social behavior and position is complex and multifactorial and will continue to face dynamic shifts (Blumstein et al. 2023; Prather et al. 2023).

In this system, stronger social ties resulted in reduced female reproductive success (Wey and Blumstein 2012), decreased hibernation survival (Yang et al. 2017) and shorter lifespans (Blumstein et al. 2018). Therefore, attributes of the environment associated with increased sociality may have downstream fitness and demographic consequences in marmots, and potentially other systems (Rézouki et al. 2016; Fisher et al. 2021; Wells et al. 2022). However, more social females experience increased summer survival in this system (Montero et al. 2020). Thus, short-term positive fitness consequences may be experienced from longer growing seasons and longer winters.

The complex and overlapping interactions between environment, sociality, and fitness are widely unknown. That is,

the fitness consequences of environmental change as mediated by sociality are poorly understood (Blumstein et al. 2023). Formal structural equation modelling may help identify the direct and indirect ways that environmental measures effect fitness by potentially acting through their effects on sociality (Blumstein et al. 2023).

Ultimately, more work is required that explores the complex relationship between the environment and seasonal timing and sociality. Future work should also more appropriately account for potential non-linear relationships in both environmental and social attributes. For example, the relationship between the environment and sociality may be mediated by age in this system as we know marmots become less social as they age (Wey and Blumstein 2010). While some work has explored the environment-sociality intersection in wild systems, very little work has explored this relationship in hibernating species. Because hibernating species are exposed to dynamic environments at multiple life-history stages (Wells et al. 2022) and may be more sensitive to environmental change and seasonal shifts than daily heterotherms (Geiser and Kenagy 1988; Geiser 2021), more research into the abiotic environment-sociality intersection in hibernators is especially needed. Further, the timing of seasons and weather are not independent given that the timing of seasonal events is influenced by a myriad of weather variables. However, our measures of seasonal timing and length had a stronger association with sociality in this system than weather patterns, which may be a consequence of the marmot's hibernation period being dictated by a multitude of intertwined weather variables. Further work teasing apart the intertwined nature of these environmental attributes and their relation to animal social behavior in the wild is required.

In summary, we have shown that the patterns of seasonal timing and length have a complex relationship with individual social behaviour and position. It is not just how long seasons are, but also the timing of seasonal events. The complex role of the abiotic environment on animal sociality demands further research across animal and social systems in our ever-changing world.

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**Data availability** Data and code to reproduce these analyses are available at <http://www.doi.org/https://doi.org/10.17605/OSF.IO/QR8XM>.

## Declarations

**Ethics approval** Data were collected under the UCLA Institutional Animal Care and Use protocol (2001–191-01, renewed annually) and with permission from the Colorado Parks and Wildlife (TR917, renewed annually). The research was in compliance with ethical guidelines and current laws of the USA and the State of Colorado.

**Author approval** All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

**Conflict of interest** We declare we have no competing interests.

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